Morphological and biometrical researches on Austrian Clausiliids. Shell morphology and variability in *Clausilia dubia* Draparnaud, 1805

Investigaciones biométricas y morfológicas en Clausílidos de Austria. Morfología y variabilidad de la concha de *Clausilia dubia* Draparnaud, 1805

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ABSTRACT

Morphological and biometrical studies on shells of some Austrian populations of *Clausilia dubia* Draparnaud, 1805, show a great variability in size and in the other morphological features within the species as a whole and also within single populations. Investigations of the variability of characters by metrical and statistical methods in some populations disclose impressive metrical divergences and morphological differences.

These results give rise to the question whether the characterization of *Clausilia dubia* as a polytypic species, as suggested by KLEMM (1960, 1973), is justified.

RESUMEN

Estudios morfológicos y biométricos en conchas de algunas poblaciones austríacas de *Clausilia dubia* Draparnaud, 1805, muestran una gran variabilidad en el tamaño y en otros caracteres morfológicos tanto en el conjunto de la especie como en poblaciones aisladas. Investigaciones sobre la variabilidad de caracteres por medio de métodos métricos y estadísticos de algunas poblaciones mestran importantes divergencias tanto métricas como morfológicas.

Estos resultados originan la pregunta de si está justificada la caracterización de *Clausilia dubia* como una especie politípica, como sugiere KLEMM (1960, 1973).

INTRODUCTION

As in great parts of Europe also in Austria, specially in the eastern parts of the Alps and in the adjacent areas, *Clausilia dubia* Draparnaud 1805 is a widely diffused and in some localities a common species that is believed to be polytypic (KLEMM, 1960, 1973; FECHTER AND FALKNER, 1990; KEARNEY, CAMERON AND JUNGBLUTH, 1983; NORDSIECK, 1990). KLEMM (1960, 1973) gave a survey of di-

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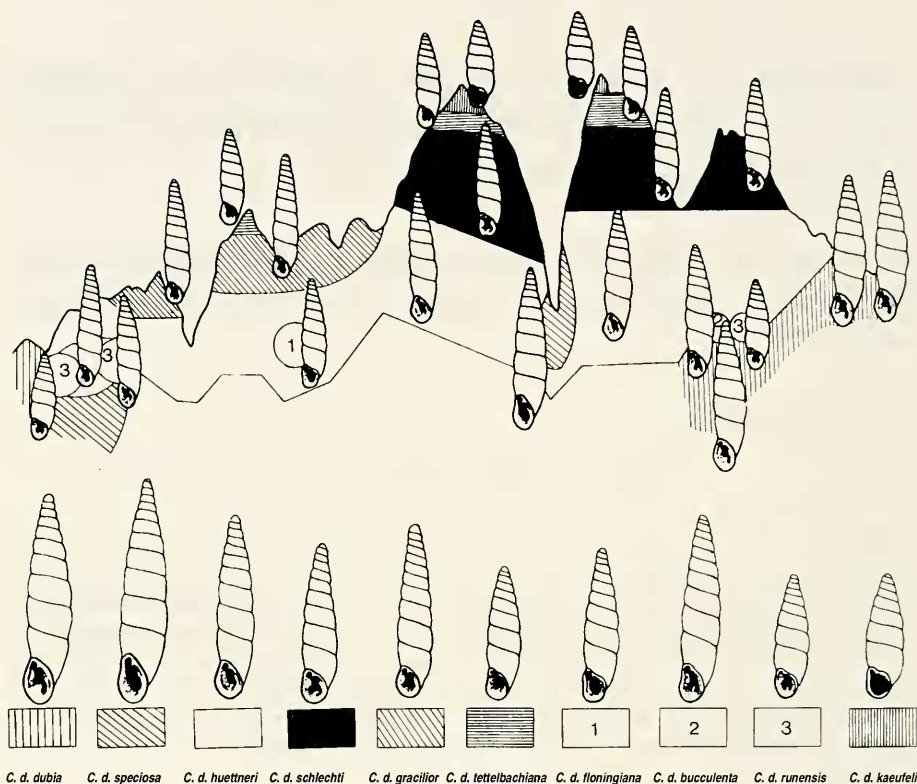
| | | | | | | | 1 | 2 | 3 | |

C. d. dubia   C. d. speciosa   C. d. huettneri   C. d. schlechti   C. d. gracilior   C. d. tettelbachiana   C. d. floningiana   C. d. bucculenta   C. d. runensis   C. d. kaeufeli

Figure 1. Distribution and vertical succession of *Clausilia dubia* subspecies as is suggested by KLEMM (1960).
Figura 1. Distribución y sucesión vertical de las subespecies de Clausilia dubia, *tal y como sugiere* KLEMM (1960).

verse "subspecies" of *Clausilia dubia* according to the characters suggested by several authors.

Traditional classification was based on a subjective selection of characters believed to be important. This classification depended on the preferences of the single authors. In some cases, subspecies are even described according to the presence of typical features in the shell of few or single specimens. HOLOYAK AND SEDDON (1988) and NORDSIECK (1990) examined some of these descriptions and offered reasonable revisions.

Some of these *Clausilia dubia* "subspecies" are considered to be widely distributed, others to be localized in small areas or subdivided into isolated populations that live in separated sites (KLEMM, 1960,

1973). Furthermore, KLEMM (1960) suggested a vertical pattern of distribution and an altitude dependent succession of diverse subspecies at the eastern ranges of the Alps (Fig. 1). He tried to explain the observed distribution pattern by probable re-immigration events in the alpine region after the Pleistocene and adaptation, enforcing the role of the environment (altitude).

Examination and possible revision of these interpretations have to critically consider the definition and the meaning of the term subspecies as it is used under various perspectives by several authors. For the practical requirement of the collector and for the taxonomic ordering of collections the technical term "subspecies" as based on peculiar morphological features
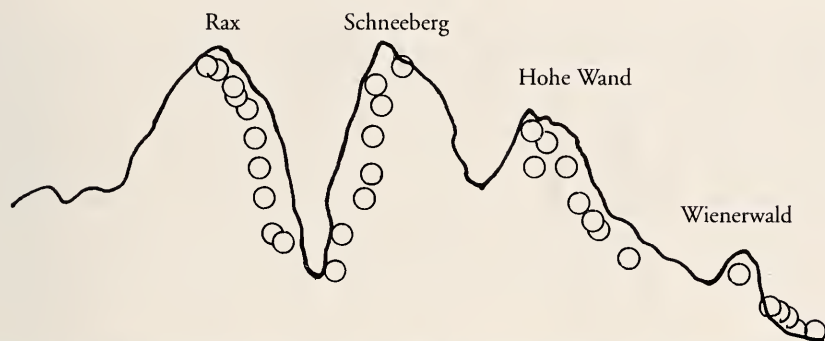
Figure 2. A profil of the estern edge of the Alps and the Wienerwald with the sample localities.
Figura 2. Perfil de la cara este de los Alpes y del Wienerwald con las localidades de muestreo.

may certainly be useful. However, it is scientifically more important to consider the conceptual background of the terminology. In the given context the concept of race or subspecies refers to biological units that are groups of related populations which are genetically characterized and, in the case of very long isolation, may be the forerunners of "valid species" (MAYR, 1967: 387; SUDHAUS AND REHFELD, 1992). This view is highly important for traditional evolutionary biology, especially in the frame of Darwinian models for evolutionary change.

In respect to the biological relevance of the subspecies concept, Sudhaus and REH-FELD (1992) are suggesting that "geographic races" (subspecies) are allopatric populations of a species, which can be distinguished taxonomically. The diagnostic characters of races should be present in 90 or more percent of individuals of the population. "

OSCHE (1994) claims that 75 percent or more members of a population must be morphologically distinguishable from the members of another population. Populations only in this case should be accepted as valid subspecies. In this paper Osche´s definition is assumed as a very tolerant and useful concept.

According to the presuppositions just given, studies referring to the subspecies problem have to treat large numbers of individuals and to apply methods of greater exactness than the usual descriptions and discriminations of characters based on

a subjective and rather arbitrary approach. It is therefore necessary to study as great a number as possible of morphological characters and to take measurements of the greatest possible exactness to establish a solid basis for statistical evaluations (NE-MESCHKAL AND KOTHBAUER, 1988; KOTH-BAUER, NEMESCHKAL, SATTMANN AND WAWRA, 1991; NEMESCHKAL, 1990, 1991, 1993; MYLONAS, KRIMBAS, TSIAKAS AND AYOUNTANTI, 1990).

Such investigations may clear up, whether the populations studied by Klemm meet all requirements of a reliable identification as subspecies (EDLINGER AND FISCHER, 1997). It is also worth while to attempt a critical revision of some samples of the Museum of Natural History in Vienna (NHMW). This paper is first attempt at elaborating a new basis for the discussion of the *Clausilia dubia* problem by morphological measurements. In future the anatomy of the soft parts and genetical analyses might be also considered.

MATERIAL AND METHODS

606 specimens of *Clausilia dubia* from different lots collected in various areas of the "Wienerwald" (Lower Austria in the southwest of Vienna) the massif of the "Hohe Wand", the "Schneeberg" and the "Rax" were investigated. The localities from which the samples came were situated at altitudes between 270 and 1850 m (Fig. 2).
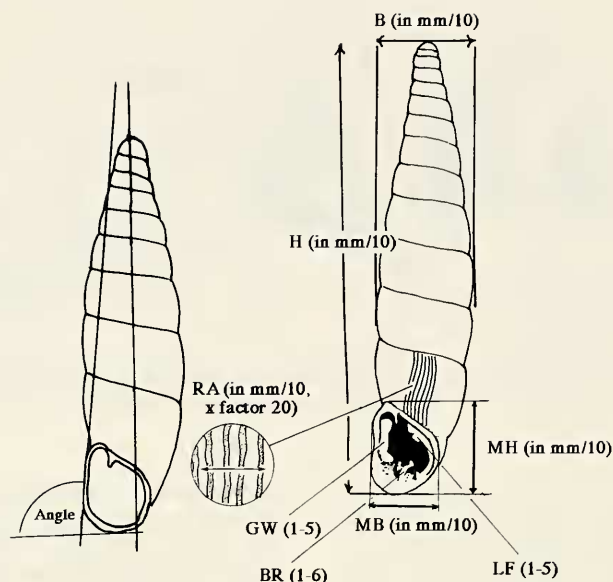
Figure 3. Measures taken from the shells: shell-height (H), shell-width (B), height (MH) and width (MB) of the aperture, distance of ribs (RA), number of whorls (WZ), angle between the spindle axis and the upper palatal (left side) (A).

Figura 3. Medidas tomadas en las conchas: altura (H), anchura (B), altura (MH) y anchura(MB) de la apertura, distancia de las estrías (RA), número de vueltas (WZ), ángulo entre el eje del huso y palatal superior (lado izquierdo) (A).

Samples (Number of Sample (Sample localities, altitude/ numbers of specimens. R = Rax: R4 (Reichenau, 700 m/1 spec.), R5 (Aufstieg z. Knappenhof, 730 m/5 spec.), R7 (Knappenhof, 800 m/24 spec.), R10 (Thörlweg, 850 m/5 spec.), R11 (Thörl-weg, 960 m/1 spec.), R12 (Thörlweg, 1120 m/29 spec.), R13 (Thörlweg, 1260 m/20 spec.), R14 (Thörlweg, 1320 m/12 spec.), R15 (Jakobskogel, 1685 m/8 spec.); S = Schneeberg: S1 (Puchberg, 560 m/15 spec.), S2 (Schneebergbahn, 750 m/57 spec.), S3 (Schneebergbahn, 790 m/5 spec.), S4 (Sch-neebergbahn, 945 m/30 spec.), S5 (Sch-neebergbahn, 1165 m/9 spec.), S6 (Schne-ebergbahn, 1370 m/6 spec.), S8 (Waxriegl ll, 1820 m/4 spec.), S9 (Waxriegl ll, 1850 m/26 spec.), S10 (Schneebergbahn, 1650 m/11 spec.), H = Hohe Wand: H1 (Dreistet-ten, 530 m/60 spec.), H2 (Einhornhöhle, 600 m/12 spec.), H3 (Drobilsteig, 700 m/24 spec.), H4 (Drobilsteig, 760 m/69 spec.), H5 (Auffahrt z. Plateau, 830 m/74 spec.), H6 (Plateau 1020 m/6 spec.), H7 (Plateau 1020 m/34 spec.), H8 (Plateau 1020 m/4 spec.); W = Wienerwald: W1 (Anninger, 400 m/11 spec.), W2 (Anninger, 450 m/4 spec.), W3 (Mödling-Klause, 260 m/8 spec.), W4 (Hu-sarentempel, 480 m/14 spec.), W5 (Auf-gang Anninger, 270 m/11 spec.), W6 (Peil-stein, 400 m/8 spec.),

Several individuals were dissected. Dissections did not reveal significant dif-ferences in the genital apparatus. 18 shells, syntypes of Austrian and South Tyrolean (Italy) localities, given in loan by the Natur-Museum Senckenberg as typical representatives of various subspe-cies were used for comparisons (Fig. 1).

They are:

1. *Clausilia dubia dubia* Draparnaud, 1805 (SMF 163024a)

2. *Clausilia dubia speciosa* A. Schmidt, 1857 (SMF 163025a)

3. *Clausilia dubia speciosa* A. Schmidt, 1857 (SMF 163026a)

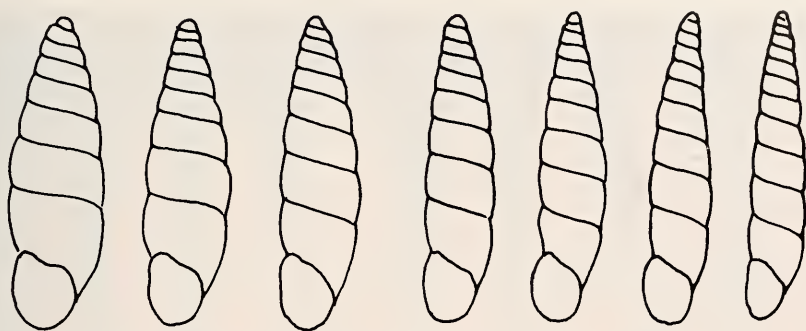4. *Clausilia dubia obsoleta* A. Schmidt, 1857(SMF 163027a)

Figure 4. Shell forms (7 stages from club-shaped -left- to spindle-shaped -right-).
Figura 4. Formas de la concha (siete estadios desde forma de maza -izquierda- hasta ahusada -derecha-).

5. *Clausilia dubia huettneri* Klemm, 1960 (SMF 1630248)

6. *Clausilia dubia schlechti* A. Schmidt, 1857 (SMF 163030a)

7. *Clausilia dubia gracilior* Clessin, 1887 (SMF 163031a)

8. *Clausilia dubia tettelbachiana* Rossmässler, 1838 (SMF 163032a)

9. *Clausilia dubia otvinensis* H. Gallenstein, 1895 (SMF 163033a)

10. *Clausilia dubia grimmeri* L. Pfeiffer, 1848 (SMF 163034a)

11. *Clausilia dubia floningiana* Tschapek, 1886 (SMF 163035a)

12. *Clausilia dubia floningiana/gracilior* (SMF 163036)

13. *Clausilia dubia bucculenta* Klemm, 1960 (Holotypus, SMF 163037)

14. *Clausilia dubia runensis* Tschapek, 1883 (SMF 163039a)

15. *Clausilia dubia moldanubica* Klemm, 1960 (Holotypus, SMF 163040)

16. *Clausilia dubia kaeufeli* Klemm, 1960 (Holotypus, SMF 163042)

17. *Clausilia dubia alpicola* Clessin, 1878 (SMF 31969)

18. *Clausilia dubia reticulata* Pini, 1883 (SMF 31936)

The shells were measured under a binocular microscope; the measurements were repeated three times. In the case of different results a special check was made. The height (H, Fig. 3) and the width (B, Fig. 3) of the shell as a whole, the height (MH, Fig. 3) and the width (MB, Fig. 3) of the aperture, the form of the aperture (MF, a series of 9 stages from pear-shaped to deltoid form, the angle between the spindle axis and the edge of the upper palatal (0.5 degree exactness), the mean of 5 rib distances (RA, Fig. 3) on the last whorl, and the number of whorls per shell (WZ, exactness: 0.25) were recorded. By comparison with stencils the morphological characters of the form of the shells (GH, a series of 7 stages from club-shaped, to extremely spindle-shaped specimens, Fig 4), the depth, and the thickness of the basal groove (BR, 6 stages, Fig. 5), the lateral internal bulge (GW, on the left side of the aperture, 5 stages of thickness (Fig. 5), and the incision in the columellar lamella (LF, 5 stages, Fig. 5) were recorded.

The measured values of the following features were processed by a WINDOWS-EXCEL 5.0 and a WINDOWS SPSS 6.0 program (BROSIUS AND BROSIUS, 1995):

- Mean of shell heights in each spot check

- Standard deviation of shell heights in each spot check

- Mean of shell heights in each spot check

- Standard deviation shell heights in each spot check

- Correlation (Pearson´s) Coefficient of all 11 values:

$$R = \frac{\sum\limits_{i=1}^{N}\left(X_i - \bar{X}\right) \cdot \left(Y_i - \bar{Y}\right)}{(N-1) \cdot S_x \cdot S_y}$$
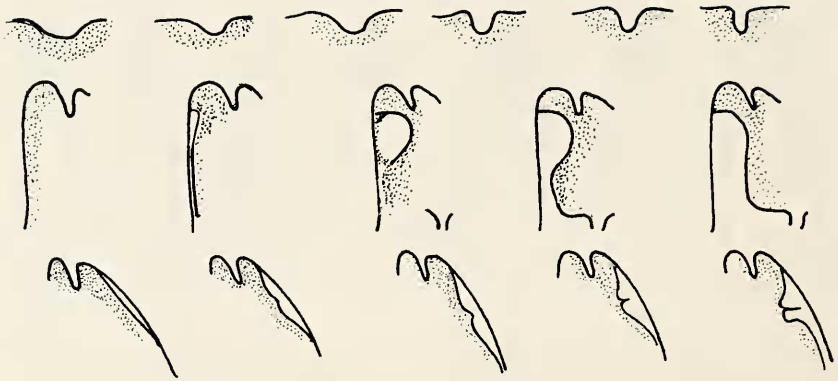
Figure 5. Basal groove (6 stages, upper row); lateral bulge (5 stages, middle row); incision in the columellar lamella (5 stages, lower row).
Figura 5. Surco basal (6 estadios, arriba); protuberancia lateràl (5 estadios, centro); incisión en la lamela columelar (5 estadios, abajo).

(R= Pearson´s Coefficient; N= number of cases; X, Y= variables; Sx, Sy= standard deviation of the variables).

By means of the WINDOWS SPSS 6.0 programs a factor extraction and a principle component analysis were executed. "Community" delivers information about the quota of spreading of one value that can be traced back to all other values. "Eigenvalue" is a value of the regression factors. It represents the quota of spreading of all values as interpreted by special regression factors. A reduction process restricts the numbers of factors in the final statistics to that exceeding 1.0. The factor matrix shows the influence of the regression factors on every variable as a percentage of 1.

The measured variables of the samples in conjunction with the values of the specimens described by KLEMM (1960) and the values of specimens of *Clausilia dubia alpicola* and *C. d. reticulata* were utilized for computing hierarchical clusters as dendrograms. For purpose of cluster analysis the measured values were transformed to "z-values", values with a mean of 0 and a standard deviation of 1. Hierarchical clusters result from dissimilarities computed on the basis of the sums of squared values of distances of each character. Thereby the spectrum of similarities and differences between all individuals of a spot check could be elaborated. The dendrograms contain specimens of various clusters according to their graduated similarity (BROSIUS AND BROSIUS, 1995).

The formula of the general distances:

$$D^2 = \sum_{i=1}^{v} \left(X_i - Y_i \right)^2$$

(D= distance; v= number of variables; X, Y= cases)

RESULTS

Means of shell height and shell width: The means of the shell height and shell width differ in all sampling areas. The lowest value was found at the "Hohe Wand" region, the highest in the "Wienerwald" area. Comparisons of the means at different altitudes reveal that KLEMM´s (1960) suggestion of a succession of different shell heights (according to a succession of "races" resp. subspecies, high values at low altitudes, low values at high altitudes) is not generally convincing (Fig. 7).

Figure 6. Two spot-checks of the collection of the NHMW (Naturhistorisches Museum, Wien). In the upper row "*Clausilia dubia schlechti*", Inv. Nr. 11. 229 NHMW. The specimen in the upper row at the left belongs to *Neostyriaca corynoides* (Held, 1836). In the row below *C. d.* "*schlechti*", Inv. Nr. 62. 348 NHMW. These spot-checks show us a high variability in the "subspecies". Scale bar 1 cm.
Figura 6. Dos muestras de la colección del NHMW (Naturhistorisches Museum, Wien). En la fila superior "Clausilia dubia schlechti", Inv. Nr. 11. 229 NHMW. El especimen de la izquierda de la fila superior pertenece a Niostyriaca corynoides (Held, 1836). En la fila inferior C. d. "schlechti", Inv. Nr. 62. 348 NHMW. Las fotografías muetran una alta variabilidad en las subespecies. Escala 1 cm.

Correlation coefficients: A very remarkable outcome of the study was a low positive correlation between the altitude and the shell height (Table I) but a high correlation between altitude and the incicion in the columellar lamella.
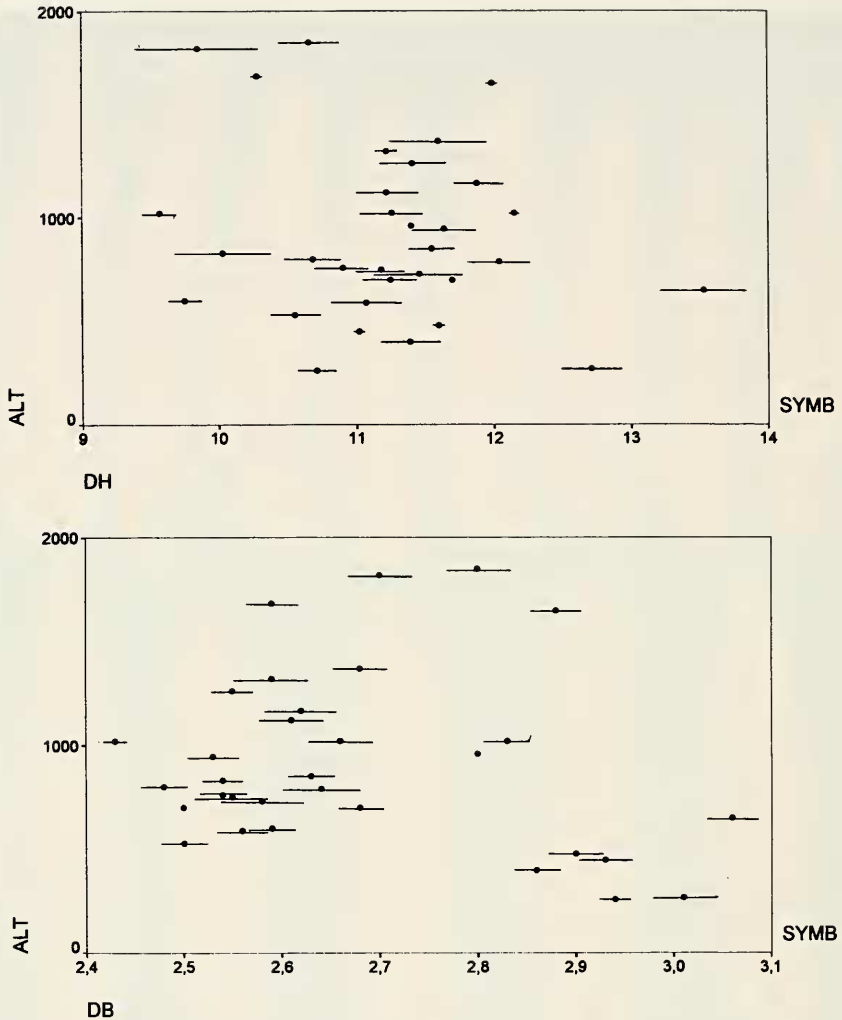
Figure 7. Scatter plots of the means of the height and width of the various samples and the altitude of sampling points.
Figura 7. Diagrama de puntos de las alturas y anchuras medias de las distintas muestras y la altitud de los puntos de muestreo.

In all four regions a significant correlation between the altitude and the height of the shells could not be confirmed. A maximum of correlation was found between shell height and the height of the aperture. Correlations between shell height and heigth of the aperture, shell height and number of whorls, shell form and number of whorls, shell form and shell height, shell height and width of the aperture, and between width of the shell and width of the aperture, are more or less remarkable. Correlation between altitude and most of the shell variables with the exception of the columellar lamella (negative correlation: -0.5123) is low (Table I).

Primary factor analysis: For the primary factor analysis all values were

Table I. Correlation coefficients (bivariate) of altitude (ALT), breadth (B), basal groove (BR), shell-form (GHF), internal bulge (GW), heighth (H), the incision in the columellar lamella (UL), width of aperture (MB), angle between the upper palatal and the spindle axis (A), height of the aperture (MH), distance of ribs (R) and number of whorls (WZ).

Tabla I. Coeficientes de correlación (bivariables) de altitud (ALT), anchura (B), surco basal (BR), forma de la concha (GHF), protuberancia interna (GW), altura (H), incisión en la lamela columelar (UL), anchura de la apertura (MB), ángulo entre el palatal superior y el eje del huso (A), altura de la apertura (MH), distancia entre las estrías (R) y número de vueltas (WZ).

	A	ALT	B	BR	GHF	GW
A	1.0000	-.0487	.1696**	.0493	.2272**	.0646
ALT	.0487	1.0000	-.0032	.1262**	-.0036	.2082**
B	.1696**	-.0032	1.0000	.1297**	.2510**	.0438
BR	.0493	.1262**	.1297**	1.0000	.0148	.3307**
GHF	.2272**	-.0036	.2510**	.0148	1.0000	.1171**
GW	.0646	.2082**	.0438	.3307**	.1171**	1.0000
H	.2011**	-.0021	.3814**	.1351**	.5258**	.1397**
LF	.0213	.5123**	.1453**	.2311**	-.0741	-.0542
MB	.0822*	.1590**	.4693**	.1606**	.0446	.1331**
MH	.0450	.0214	.5417**	.1644**	.0656	.1621**
R	.1370**	.1850**	.0931*	-.0704	.2172**	.1103**
WZ	.2812**	.1711**	.0127	.0745	.5760**	.0632

	H	LF	MB	MH	R	WZ
A	.2011**	.0213	.0822*	.0450	.1370**	.2812**
ALT	.0021	.5123**	.1590**	.0214	.1850**	.1711**
B	.3814**	.1453**	.4693**	.5417**	.0931*	.0127
BR	.1351**	.2311**	.1606**	.1644**	-.0704	.0745
GHF	.5258**	-.0741	.0446	.0656	.2172**	.5760**
GW	.1397**	-.0542	.1331**	.1621**	.1103**	.0632
H	1.0000	.0780	.4968**	.7071**	.1411**	.6663**
LF	.0780	1.0000	.2288**	.0913*	.1501**	.0891*
MB	.4968**	.2288**	1.0000	.5965**	-.0230	.1733**
MH	.7071**	.0913*	.5965**	1.0000	-.0412	.2455**
R	.1411**	.1501**	-.0230	-.0412	1.0000	.2058**
WZ	.6663**	.0891*	.1733**	.2455**	.2058**	1.0000

*= Signif. LE .05;**= Signif. LE .01 (2-tailed)

used irrespective of the altitude. The analyses result four factors with an Eigenvalue of more than 1.0. One analysis was done including the NMS specimens (Table II), the other only with the own samples (Table III). The results of both analyses were corresponding at a high degree.

Factor 1 has a significant influence on the width of the shell, the shell height, the width of the aperture, the height of the aperture and the number of whorls.

Factor 2 has a significant influence on the angle between the axis and the left palatal, the width of the aperture, the rib distance and the number of whorls, factor

Table II. Primary component analysis factors of all samples including the NMS specimens. Abbreviations as in Table I.
Tabla II. Factores del análisis de componentes principales de todas las mustras incluyendo los ejemplares NMS. Abreviaturas como en la Tabla I.

| | | Initial Statistics | | | |
Variable	Communality	Factor	Eigenvalue	Pct of Var	Cum Pct
A	1.00000	1	3.14275	31.4	31.4
B	1.00000	2	1.48937	14.9	.46.3
BR	1.00000	3	1.34787	13.5	59.8
GW	1.00000	4	1.09305	10.9	70.7
H	1.00000	5	.81589	8.2	78.9
LF	1.00000	6	.69772	7.0	85.9
MB	1.00000	7	.54068	5.4	91.3
MH	1.00000	8	.42572	4.3	95.5
R	1.00000	9	.32418	3.2	98.8
WZ	1.00000	10	.12276	1.2	100.0

PC extracted 4 factors

| | Factor Matrix | | | |
	Factor 1	Factor 2	Factor 3	Factor 4
A	.24107	-.39349	.57325	-.01561
B	.64730	.28942	-.49248	-.01712
BR	.19488	.59543	.52902	.22231
GW	.11069	.50354	.53469	-.34493
H	.89714	.19205	.07467	-.16390
LF	.25618	.22266	.08430	.85909
MB	.75790	.21202	-.17180	.03663
MH	. 85718	. 10931	-.19219	-.16564
R	.24758	.55811	.01044	.35599
WZ	.61193	-.43340	.36292	-.06089

| | | Final Statistics | | | |
Variable	Communality	Factor	Eigenvalue	Pct of Var	Cum Pct
A	.54182	1	3.14275	31.4	31.4
B	.74559	2	1.48937	14.9	46.3
BR	.72179	3	1.34787	13.5	59.8
GW	.67067	4	1.09305	10.9	70.7
H	.87418				
LF	.86036				
MB	.65022				
MM	.81108				
R	.49962				
WZ	.69772				

Skipping rotation 1 for extraction 1 in analysis 1

Table III. Primary component analysis factors of all samples excluding the NMS specimens. Abbreviations as in Table I.
Tabla III. Factores del análisis de componentes principales excluyendo los ejemplares NMS. Abreviaturas como en la Tabla I.

Variable	Communality	Factor	Eigenvalue	Pct of Var	Cum Pct*
		Initial Statistics			
A	1.00000	1	2.98596	29.9	29.9
B	1.00000	2	1.52656	15.3	45.1
BR	1.00000	3	1.27032	12.7	57.8
GW	1.00000	4	1.19526	12.0	69.8
H	1.00000	5	.79324	7.9	77.7
LF	1.00000	6	.70682	7.1	84.8
MM	1.00000	7	.56029	5.6	90.4
MM	1.00000	8	.45357	4.5	94.9
R	1.00000	9	.36803	3.7	98.6
WZ	1.00000	10	.13995	1.4	100.0

PC extracted 4 factors

	Factor 1	Factor 2	Factor 3	Factor 4
		Factor Matrix		
A	.19408	.61541	.28529	-.11267
B	.60129	-.52606	-.27656	.02153
BR	.32508	-.17128	.64145	.42482
GW	.25481	-.15515	.76411	-.07054
H	.86917	.22511	-.06761	-.24429
LF	.28165	.05486	-.10404	.82738
MM	.74584	-.22587	-.11384	.04898
MM	.83214	-.22388	-.10785	-.18500
R	.18873	.53391	-.27470	.43010
WZ	.54499	.61465	.04084	-.17555

Variable	Communality	Factor	Eigenvalue	Pct of Var	Cum Pct
		Final Statistics			
A	.51047	1	2.98596	29.9	29.9
B	.71523	2	1.52656	15.3	45.1
BR	.72695	3	1.27032	12.7	57.8
GW	.67784	4	1.19526	12.0	69.8
H	.87038				
LF	.77771				
MM	.62266				
MM	.78843				
R	.58114				
WZ	.70730				

Skipping rotation 1 for extraction 1 in analysis 1

Figure 8. Bar charts of factor 1 and 2 (spot checks differentiated).
Figura 8. Diagrama de barras de los factores 1 y 2 (pruebas diferenciadas).

on the basal groove and factor 4 has a significant influence on the columellar lamella.

Bar charts show us the distributions and the maximum of the values of the primary factors in the samples for comparison.

The values of factor 1 have a similar distribution in the Schneeberg, the Rax and the Hohe Wand area and another distribution pattern with another maximum in the Wienerwald area (Fig. 8).

The values of factor 2 show us a very similar distribution in the Rax and the Schneeberg area, but other patterns in the Hohe Wand and the Wienerwald area (Fig. 8).

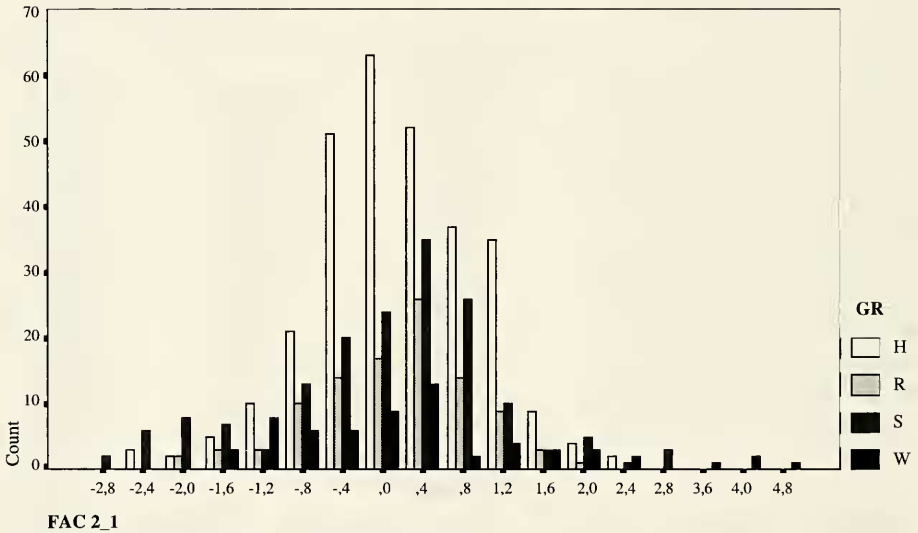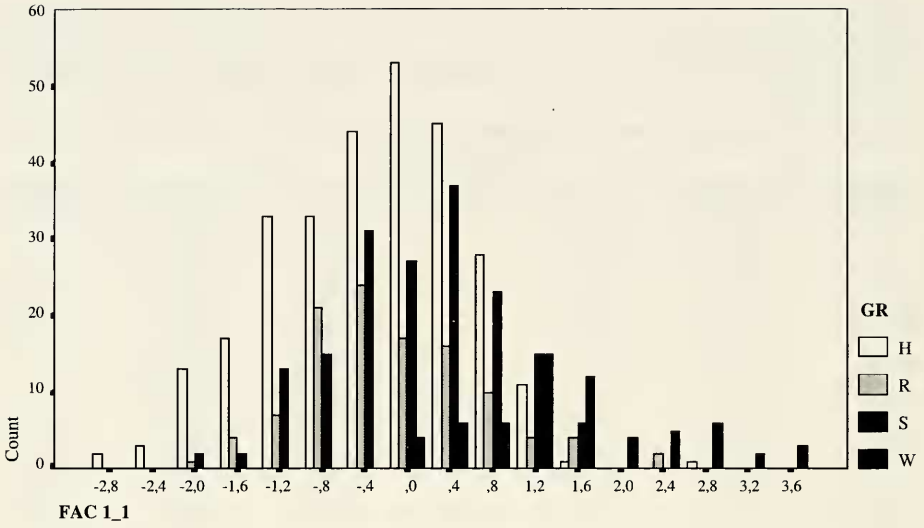Factor 3 has similar distributions of values in the samples of Rax, Schneeberg
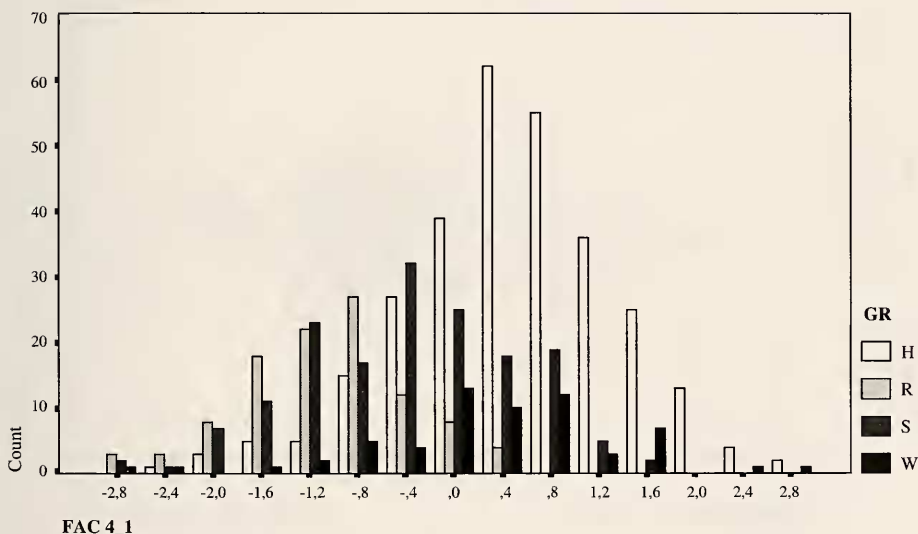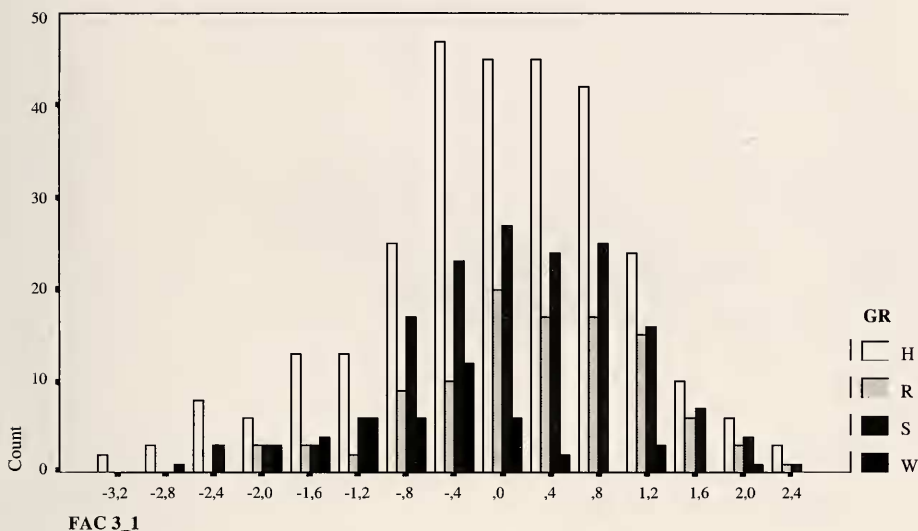
Figure 9. Bar charts of factor 3 and 4 (spot checks differentiated).
Figura 9. Diagrama de barras de los factores 3 y 4 (pruebas diferenciadas).

and Hohe Wand, but another maximum in the Sample of the Wienerwald area (Fig. 9).

Diagrams of the values of factor 4 show us different distributions in all samples (Fig. 9).

A two dimensional scatter plot of factor 1 and factor 2 for a comparison of the samples of the four areas (Fig. 10)

shows us, that by the positions of the specimens and by their pattern of distribution only two partially different groups can be distinguished: one group consisting of specimens of the Hohe Wand, the Schneeberg and the Rax area at the one side and a second group with the specimens from the Wienerwald area at the other. Both groups are overlapping.
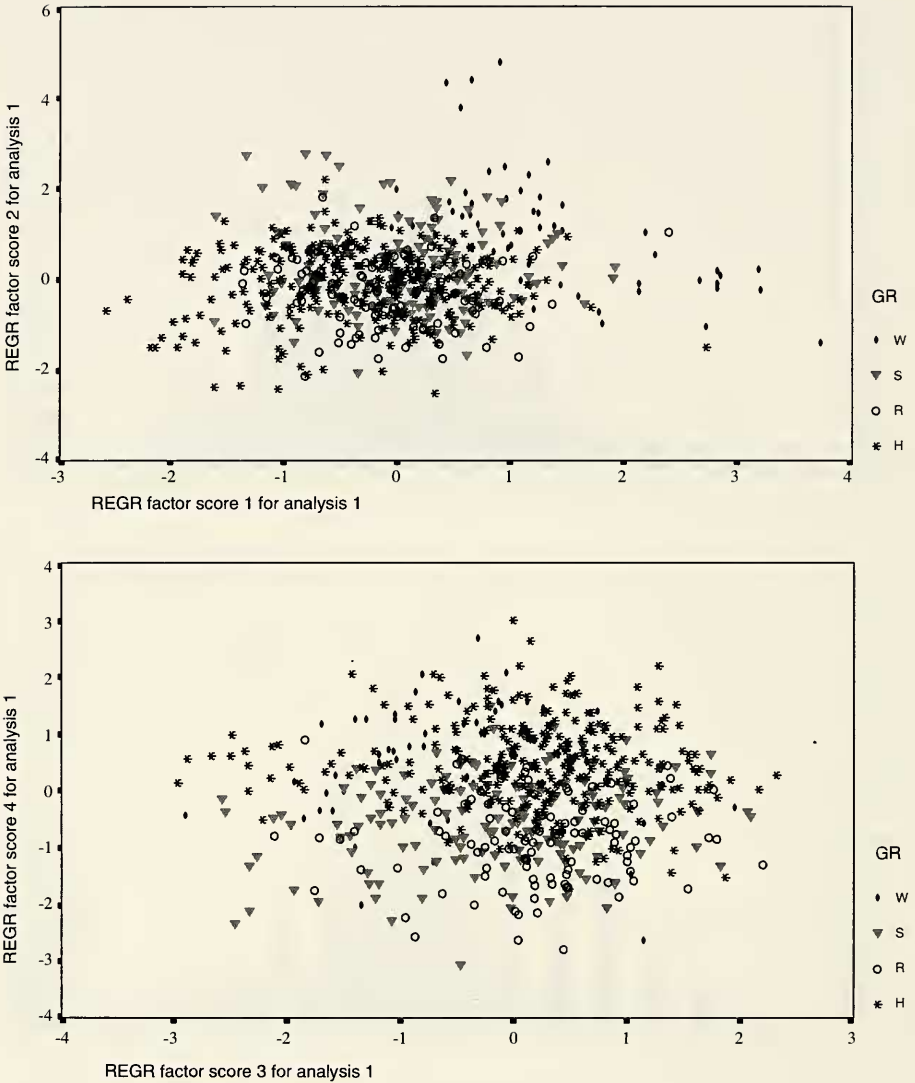
Figure 10. Scatter plots of the samples with value 1 and 2, 3 and 4 (spot checks differentiated).
Figura 10. Diagramas de puntos de las muestras con los valores 1 y 2, 3 y 4 (pruebas diferenciadas).

A scatter plot with factor 3 and factor 4 (Fig. 10) shows us a wide distribution of the specimens of the Schneeberg area and a partial separation of the samples of the Rax area at the one and the samples of the Hohe Wand and the Wienerwald area at the other side. Also these distribution areas of the samples are overlapping at a high degree.

Scatter plots of regression factor 1 and 2 of all samples including the SMF specimens based on three morphologically important measures (Fig. 11) discloses a remarkable morphological isolation of some SMF specimens, especially of those specimens assigned to *Clausilia dubia speciosa, C. d. dubia, C. d. floningiana* and *C. d. floningiana/gracilor, C. d. graci-*
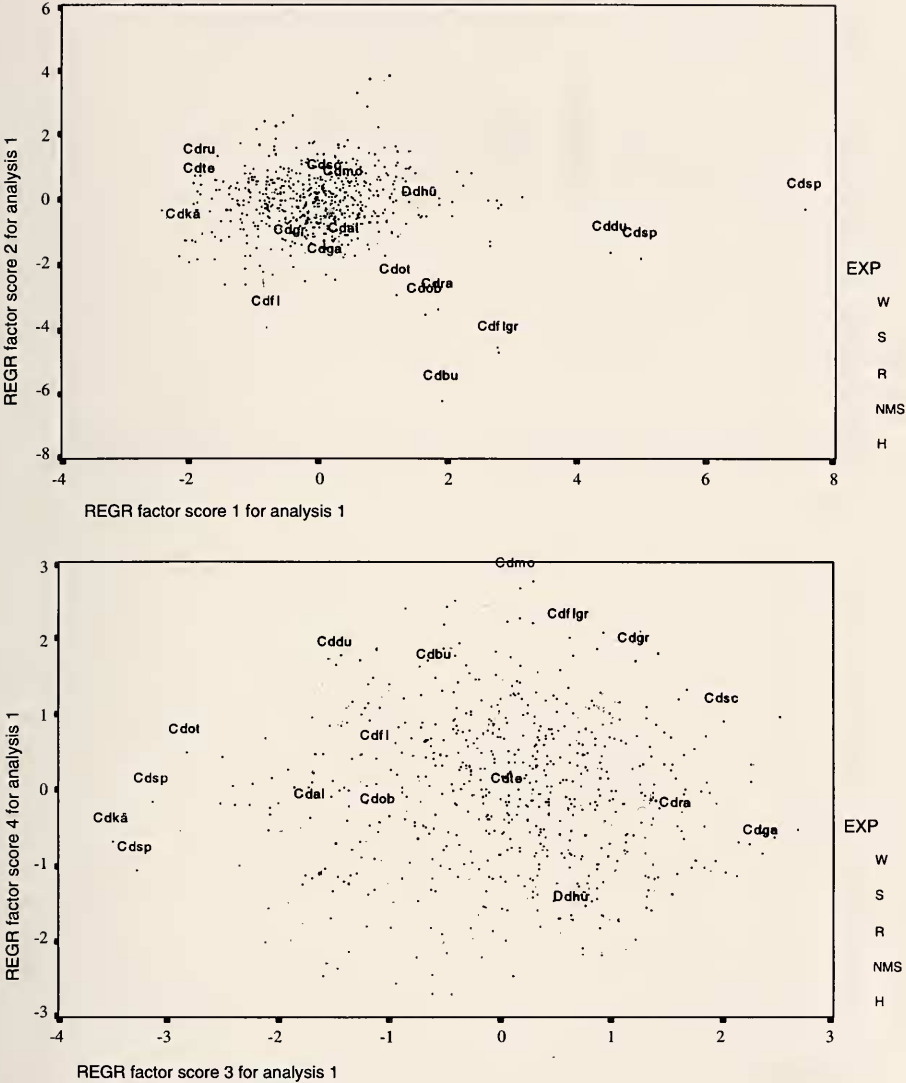
Figure 11. Scatter plots of the samples and the NMS specimens with value 1 and 2, 3 and 4 (points represent samples, NMS specimens with abbreviations).
Figura 11. Diagramas de puntos de las muestras y los especímenes NMS con valores 1 y 2, 3 y 4 (los puntos representan las muestras, los especímenes NMS son las abreviaturas).

lior, *C. d. grimmeri*, and also *C. d. bucculenta*. These specimens are found outside the central area of distribution of the two dimensional coordinate system of the scatter plot, where the bulk of specimens appears in a high concentration.

A scatter plot of the factors 3 and 4 (Fig. 11) shows us more peripheral positions of *Clausilia dubia moldanubica*, *C. d. otvinensis*, *C. d. speciosa*, *C. d. kaeufeli*, *C. d. gracilior*, *C. d. schlechti*, *C. d. grimmeri* and *C. d. floningiana/gracilior*.

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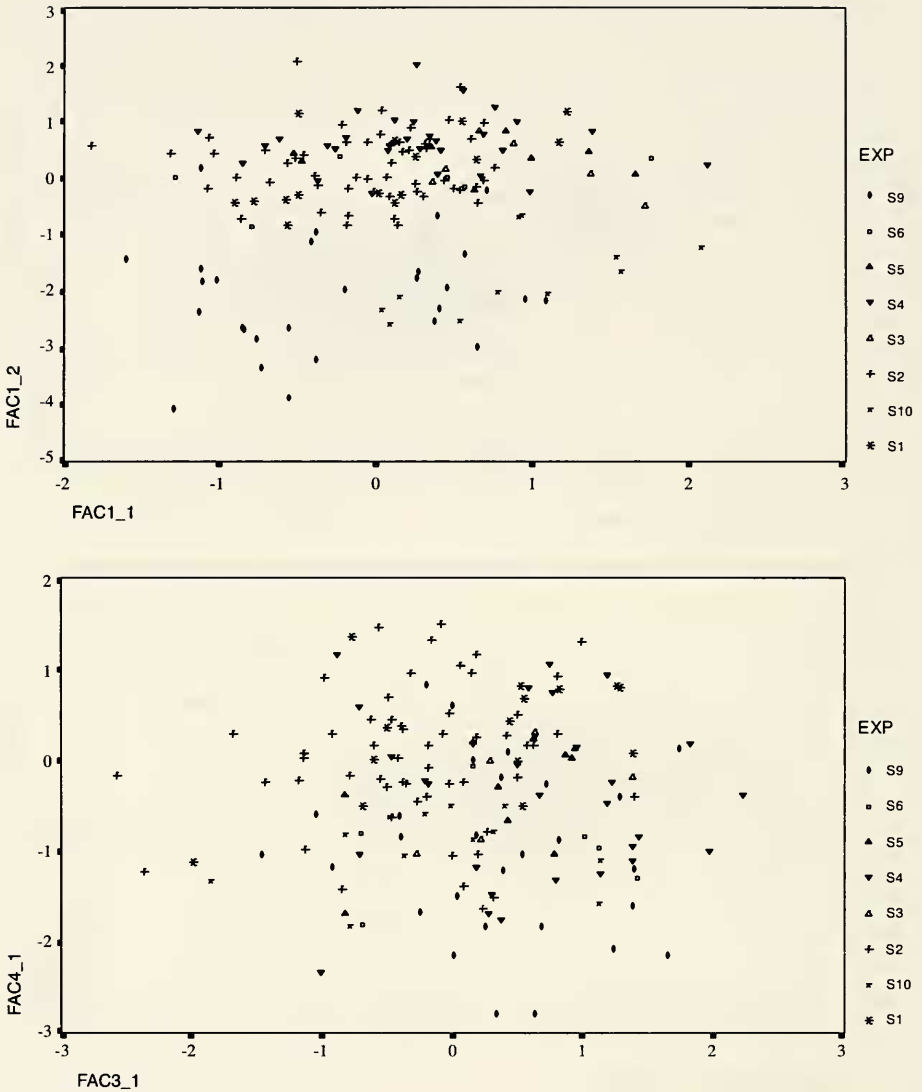
Figure 12. Two-dimensional scatter plots with factors 1/2 and 3/4 of a spot check of the Schneeberg samples (see the altitude of the sample areas at Material and methods).
Figura 12. Diagramas de puntos de dos dimensiones con factores 1/2 y 3/4 de las muestras de Schneeberg (ver la altitud de las áreas de muestreo en Material y métodos).

Scatter plots of the factors 1 to 4 of the various samples of the Schneeberg area (from different altitudes) disclose no remarkable dependence of the factors 1, 3 and 4 on altitude (Fig. 12).

Factor 2 shows us a separate distribution of values of sample S9 (1850 m) and S10 (1650 m). The distribution areas of the other samples are covering one another. They are overlapping distribution areas of sample S9 and S10 insignificantly.

A scatter plot of the Rax samples (Fig. 13) which were arranged in correspondence to the altitude in three groups
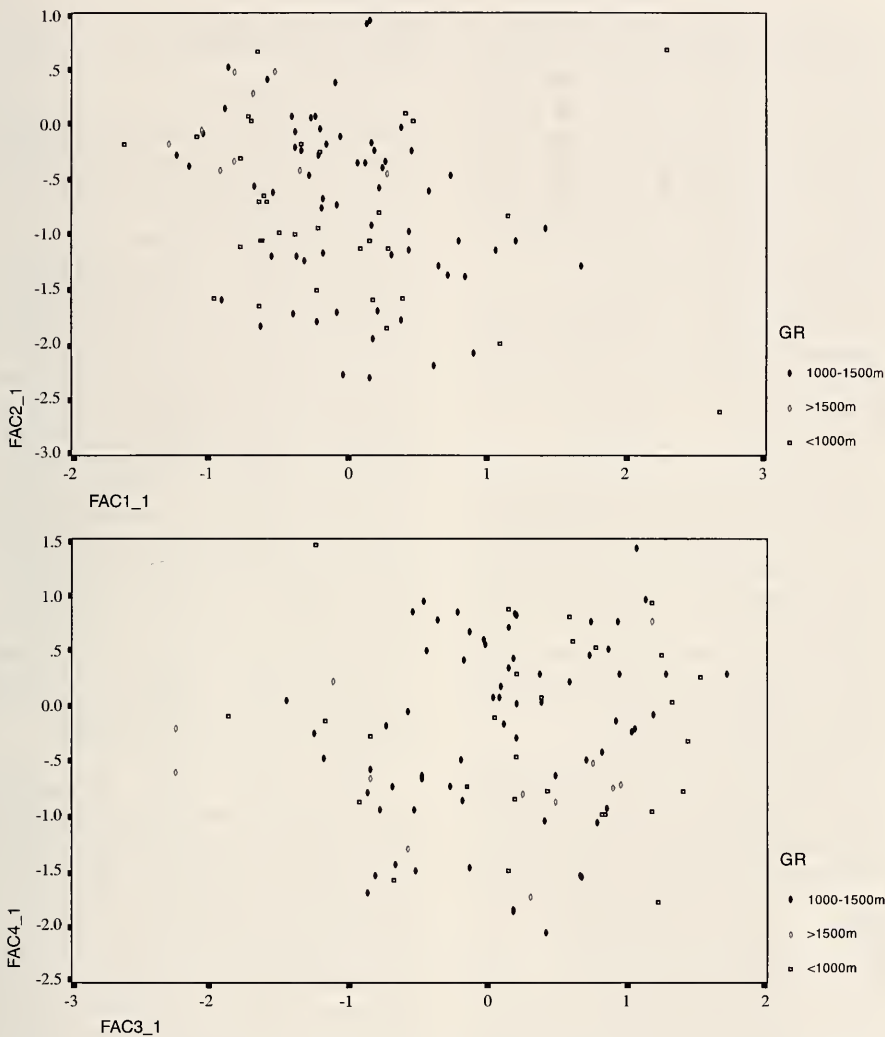
Figure 13. Two-dimensional scatter plots with factors 1/2 and 3/4 of a spot check of the Rax samples, arranged in three groups in accordance with the altitude of the sample areas (less 1000 m, 1000-1500 m, more than 1500 m).
Figura 13. Diagramas de puntos de dos dimensiones con factores 1/2 y 3/4 de las muestras de Rax , ordenadas en tres grupos de acuerdo con la altitud de las áreas de muestreo (menos de 1000 m, 100-1500 m, más de 1500 m).

(less than 1000m, 100-1500m, more than 1500m) results no altitude dependence of the factors.

Cluster analysis: For the first cluster analysis the measured values were taken from a group of specimens which

consisted of selected samples from different localities and altitudes; data from the SMF specimens were also included (Fig. 14). The hierarchical cluster which is presented as a dendrogram contains groups of different size which were collected at different localities.

Notable is the isolated position of the SMF specimens of *Clausilia dubia speciosa* and *C. d. dubia* which constitute a cluster of their own together with two specimens of the samples. Almost the same phenomena occur in dendrograms of samples collected in the areas "Hohe Wand", "Schneeberg" and "Rax". In these cases specimens of the SMF were also taken into consideration.

In general the clusters show remarkable segregations. Similarities of the individuals coming out from the same locality and appearing together in clusters may be seen as indication of close relationship.

At the other side the spot checks from various areas are overlapping at a high degree. Relevant portions of individuals, which present all the characters of several "subspecies" (subspecies seen in the traditional way) do not occur. It is remarkable that most specimens from the SMF which were considered to be typical for specific regions, appear also in the different branches of the dendrograms and in various clusters.

Only the SMF specimens of *Clausilia dubia speciosa*, and in a most astonishing way, the SMF specimen of *C. d. dubia*, an individual belonging to the nominotypical subspecies" are seen at own separate branches of the dendrograms. This finding is in full agreement with the above mentioned scatter plots of the analysis of the main components. All three above mentioned specimens are characterized by strongly deviating measures and stand in isolated positions. It is evident that this finding disa-

grees with the geographical distribution shown in the literature (KLEMM, 1960).

Wienerwald: The samples from the Wienerwald area come from altitudes between 270 and 400 m and sites similar in climate and ecological conditions (fir, pine, and mixed forests).

The shells are rather similar and club shaped, but differ considerably in shell height and width, height and width of aperture, and distance of ribs. The same is true for all the other measures taken. In the hierarchical cluster analysis of samples from the Wienerwald area (Fig. 15) which was considered to be the type locality of *Clausilia dubia dubia*, the position of *C. d. dubia*, *C. d. kaeufeli*, and *C. d. speciosa* is found to be extremely isolated in a cluster of their own (Fig. 16). Within the second cluster also other SMF specimens appear in entirely isolated branches. Only *C. d. runensis*, *C. d. tettelbachiana*, *C. d. grimmeri*, *C. d. schlechti* and *C. d. moldanubica* appear in a branch together with the specimens of the samples from the Wienerwald area.

Hohe Wand: Analyses of samples taken from the Hohe Wand (altitude between 560 m and 1080 m; Fig. 16) also lead to results which are not in accordance with generally held views. *Clausilia dubia speciosa* and *C. d. runensis* are in an isolated position. They are in a cluster of their own together with one specimen of the local sample from H8. Also *C. d. bucculenta*, *C. d. floningiana/gracilior*, *C. d. floningiana*, *C. d. reticulata*, *C. d. obsoleta*, *C. d. gracilior*, *C. d.*

(Right page). Figure 14. Hierarchical cluster of a spot-check of all samples and the SMF specimens (Wi-y= specimens of the Wienerwald area; i= sample; y= number of the specimen; Hi-y= specimens of the Hohe Wand area; Si-y= specimens of the Schneeberg area; Ri-y= specimens of the Rax area; Cd-= specimens of the SMF: du= *dubia*; sp= *speciosa*; ob= *obsoleta*; hn= *huettneri*; sc= *schlechti*; gr= *gracilior*; te= *tettelbachiana*; ot= *otvinensis*; gi= *grimmeri*; fl= *floningiana*; flgr= *floningiana/gracilior*; bu= *bucculenta*; ru= *runensis*; mo= *moldanubica*; kä= *kaeufeli*; al= *alpicola*; re= *reticulata*).

(Página derecha). Figura 14. Cluster de todas las muestras y los especímenes SMF (Wi-y= especímenes del área de Wienerwald; i= muestra; y= número del especimen; Hi-y= especímenes del área de Wand; Si-y= especímenes del área de Schneeberg; Ri-y= especímenes del área de Rax; Cd-= especímenes SMF: du= dubia; sp= speciosa; ob= obsoleta; hn= huettneri; sc= schlechti; gr= gracilior; te= tettelbachiana; ot= otvinensis; gi= grimmeri; fl= floningiana; flgr= floningiana/gracilior; bu= bucculenta; ru= runensis; mo= moldanubica; kä= kaeufeli; al= alpicola; re= reticulata).

Rescaled Distance Cluster Combine

```
Rescaled Distance Cluster Combine

    C A S E      0         5        10        15        20
    Label  Num   +---------+---------+---------+---------+---

    W1       6
    W1       7
    W1       3
    W1       4
    W4      33
    W1       5
    W2      12
    W4      27
    W3      23
    W1       2
    W4      30
    W4      29
    W3      24
    Cdmo    73
    W3      18
    W3      20
    W2      14
    W4      39
    W3      19
    W4      38
    W2      16
    W2      17
    W3      22
    W4      31
    W4      32
    W4      28
    W4      34
    W3      21
    W4      36
    W5      50
    W3      25
    W4      37
    W4      35
    W2      13
    W5      42
    W5      40
    W5      41
    W2      15
    W1       1
    W5      44
    W5      45
    W5      48
    W6      52
    W5      47
    W6      55
    W6      56
    W6      53
    W6      54
    W5      43
    W4      26
    W5      46
    W5      49
    W6      51
    W1       8
    W1      11
    W1      10
    W1       9
    Cdsc    64
    Cdgi    68
    Cdte    66
    Cdru    72
    W6      57
    W6      58
    Cdflgi  70
    Cdbu    71
    Cdga    65
    Cdre    76
    Cdob    62
    Cdhn    63
    Cdot    67
    Cdal    75
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    Cdfl    69
    Cddu    59
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    Cdsp    60
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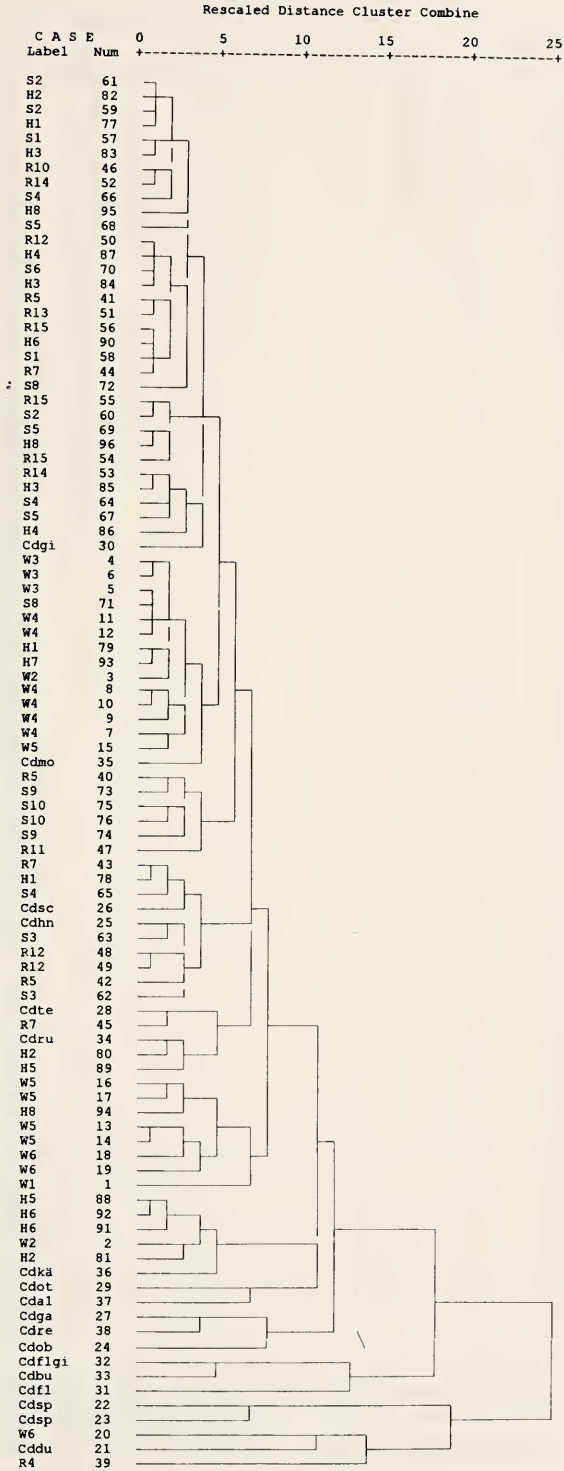
Figure 15. Hierarchical cluster of a spot check of all samples of the Wienerwald area and the SMF specimens. Abbreviations as in Figure 14.

Figura 15. Cluster de todas las muestras del área de Wienerwald y los especímenes SMF. Abreviaturas como en la Figura 14.
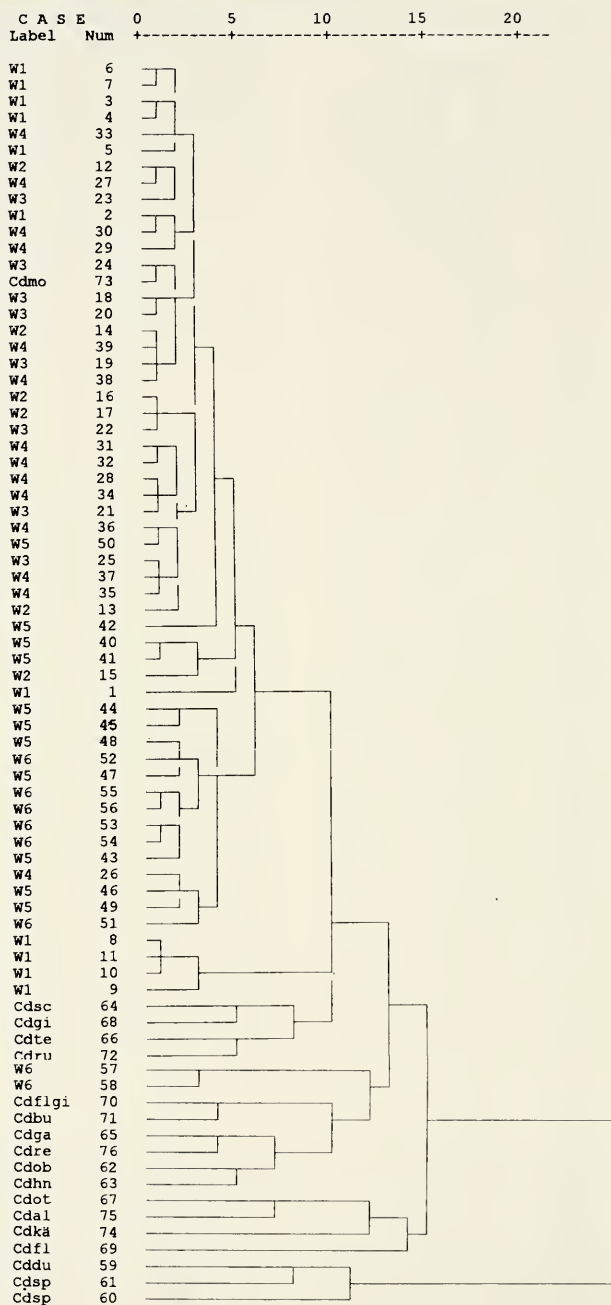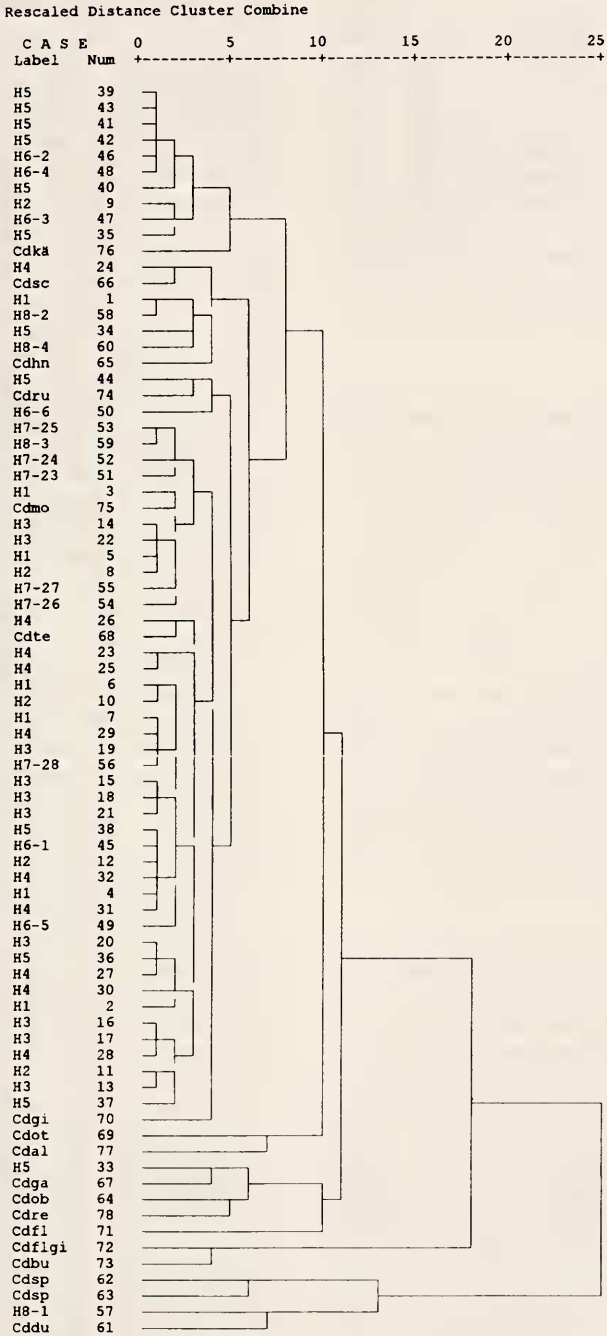
Figure 16. Hierarchical cluster of a spot check of all samples of the Hohe Wand area and the SMF specimens. Abbreviations as in Figure 14.
Figura 16. Cluster de todas las muestras del área de Hohe Wand y los especímenes SMF. Abreviaturas como en la Figura 14.

alpicola, C. d. otvinensis and *C. d. grim-meri* occur in separated branches and only *C. d. tettelbachiana, C. d. moldanu-bica, C. d. huettneri* and *C. d. kaeufeli* are integrated in branches together with the major part of the specimens from the Hohe Wand area. There are no indications of the succession postulated by former workers (KLEMM, 1960) when one takes into consideration altitudes of the localities from which they came and the similarities that appear in the dendrogram.

Schneeberg: The studied material was collected at altitudes between 700 to 1850 m. The cluster analysis (Fig. 17) reveals morphologically isolated positions for *Clausilia dubia speciosa, C. d. dubia, C. d. kaeufeli, C. d. floningiana, C. d. reticulata, C. d. obsoleta, C. d. bucculenta, C. d. floningiana/gracilior, C. d. alpicola, C. d. otvinensis, C. d. tettelbachiana, C. d. runensis* and *C. d. moldanubica*. Only *C. d. grimmeri, C. d. gracilior* and *C. d. schlechti* occur in branches together with most of the specimens of the Schneeberg spot checks. Remarkable is that specimens with close morphological relations to *C. d. kaeufeli*, as expected for the peak of the mountain, don't occur in the clusters. The SMF specimen of *C. d. kaeufeli* is isolated in the dendrogram.

Rax: The studied material was collected at altitudes between 700 to 1685 m. As in the Clusters analyses of the other areas *Clausilia dubia dubia,* and *C. d. speciosa* are isolated in a Cluster of ist own (Fig. 18). Also *C. d. kaeufeli, C. d. floningiana, C. d. bucculenta, C. d. floningiana/gracilior, C. d. runensis, C. d. alpicola, C. d. otvinensis, C. d. otvinensis, C. d. obsoleta, C. d. reticulata* and *C. d. gracilior* occur very isolated in branches together with only few specimens of the local samples. Only *C. d. grimmeri, C. d. moldanubica, C. d. tettelbachiana, C. d. schlechti* and *C. d. huettneri* can be seen as well integrated in clusters with the major part of the local samples. No remarkable position of *C. d. kaeufeli* or a succession as suggested by Klemm was visible.

DISCUSSION AND CONCLUSION

The conclusions presented here must be seen as being valid only for samples of *Clausilia dubia* collected in restricted areas. Only further research might lead to conclusive results on possible geographic variation in *C. dubia*.

The results of the present research as well as a critical evaluation of those of earlier researchers show us the limits inherent the intuitive, subjective method used in the analysis of characters. Earlier studies by EDLINGER AND MILDNER (1979) on *Clausilia dubia* in *Carinthia*, using traditional morphological methods based on a number of shell characters, also showed a high variability of most of these characters within each population. This may be a common phenomenon when analyses are based on a large number of characters. In this case, techniques of measurement, as well as applied statistical methods might present potential sources of error.

Nevertheless, all observations are indicative of high variability within the species. Similar observations can be made in many of the collection samples (Fig. 6). This can be clearly discerned, in spite of the fact that many of these samples have been classified as belonging to various subspecies.

To gain a better understanding of shell variability, we must also consider the influence of ecological factors, and the life history of the specimens. Morphological features may be influenced by non hereditary factors too (GOODFRIEND, 1986).

Against the background of low correlation coefficients between altitude and most characters, except columellar lamella, altitude in itself cannot be conceived as an substantial ecological factor, because the measures of the shells except the columellar lamella don't vary significantly in correlation with altitude. A reason for the remarkable correlation of altitude with the columellar lamella might be that the *Clausilia dubia* shells of the Wienerwald area commonly have very pregnant incisions of the columellar lamella.

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          Rescaled Distance Cluster Combine

      C A S E      0        5        10        15        20        25
      Label   Num  +--------+---------+---------+---------+---------+
        S4     26
        S4     29
        S4     25
        S5     33
        S1      2
        S5     34
        S3     21
        S1      4
        S1      5
        S2     12
        S2     17
        S3     22
        S5     35
        S6     41
        S6     39
        S2      6
        S5     36
        S1      1
        S5     37
        S2     14
        S6     42
        S3     19
        S6     38
        S2     10
        S3     18
        S4     27
        S5     30
        S2      8
        S2     11
        S2      7
        S2     13
        S2     15
        S5     32
        S6     40
        S2      9
        S3     20
      Cdsc     66
        S2     16
        S4     28
      Cdhn     65
        S4     23
        S4     24
      Cdga     67
      Cdgi     70
        S9     50
        S9     51
        S9     53
        S9     52
        S5     31
        S9     55
       S10     57
       S10     56
       S10     58
       S10     60
        S9     54
        S9     47
        S9     48
        S9     46
        S1      3
        S8     45
        S9     49
        S6     43
        S8     44
      Cdmo     75
      Cdru     74
      Cdte     68
       S10     59
      Cdot     69
      Cdal     77
      Cdflgi   72
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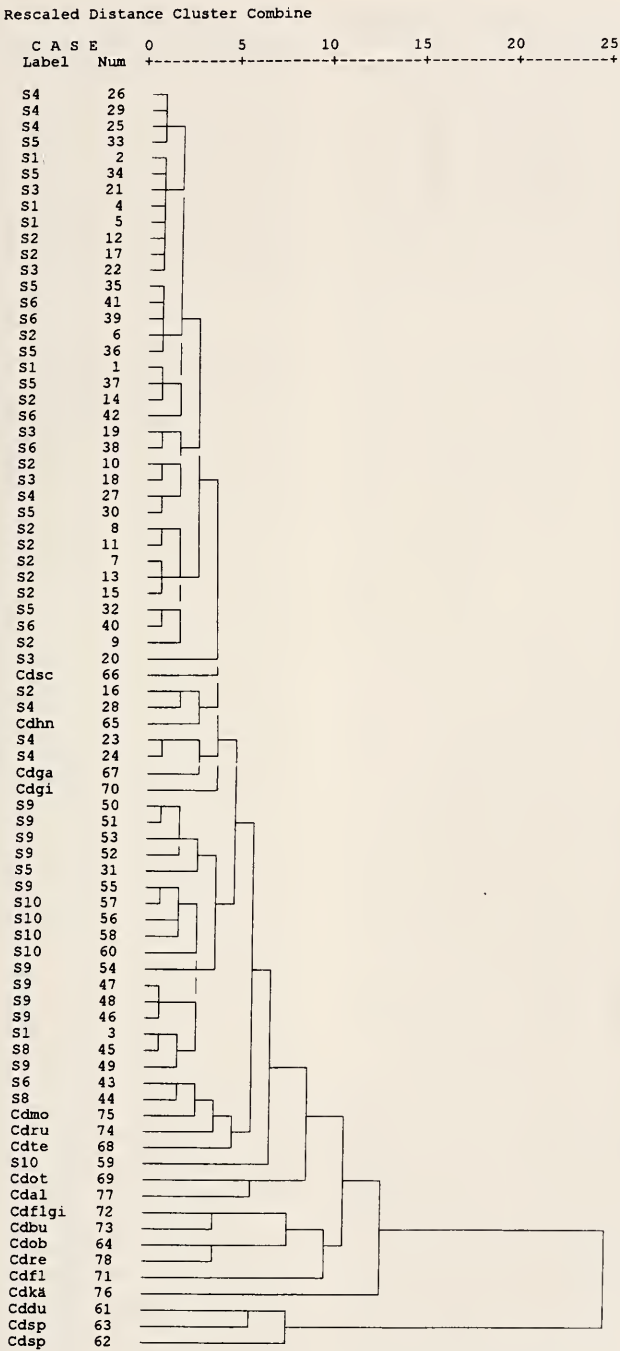
Figure 17. Hierarchical cluster of a spot check of all samples of the Schneeberg area and the SMF specimens. Abbreviations as in Figure 14.

Figura 17. Cluster de todas las muestras del área de Schneeberg y los especímenes SMF. Abreviaturas como en la Figura 14.

```
Rescaled Distance Cluster Combine

    C A S E        0         5        10        15        20        25
  Label   Num      +---------+---------+---------+---------+---------+

  R15      53       ─┐
  R15      54       ─┤
  R7       16       ─┤
  R12      28       ─┤
  R15      55       ─┤
  R7       18       ─┼┐
  R12      27       ─┘│
  R13      32       ─┐│
  R15      52       ─┤│
  R5        3       ─┤│
  R12      26       ─┤│
  R5        4       ─┤│
  R14      39       ─┘│
  R13      30       ─┐│
  R13      34       ─┤│
  R13      33       ─┤│
  R13      35       ─┼┘
  R13      36       ─┤
  R13      37       ─┤
  R7       14       ─┤
  R7       15       ─┘
  R10      20       ─┐
  R13      31       ─┤
  R14      44       ─┘
  R14      46       ─┐
  R14      47       ─┼┐
  R14      41       ─┤│
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  R14      43       ─┘│
  R15      50       ──┤
  R15      51       ──┘
  R7        7       ─┐
  R7       13       ─┤
  R10      21       ─┤
  R14      38       ─┤
  R12      23       ─┼┐
  R13      29       ─┤│
  R12      24       ─┤│
  R12      25       ─┘│
  R7        8       ─┐│
  R7       10       ─┼┤
  R5        5       ─┤│
  R5        6       ─┘│
  Cdhn     60       ──┤
  R7       11       ─┐│
  R7       12       ─┼┤
  R7        9       ─┘│
  R14      40       ──┤
  Cdsc     61       ──┤
  R7       19       ─┐│
  Cdte     63       ─┘│
  R14      45       ─┐│
  R14      49       ─┤│
  R14      48       ─┼┘
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  Cdgi     65       ─┘
  R5        2       ─┐
  R7       17       ─┼┐
  R11      22       ─┘│
  Cdga     62       ──┤
  Cdre     73       ──┤
  Cdob     59       ──┤
  Cdot     64       ──┤
  Cdal     72       ──┤
  Cdru     69       ──┤
  R4        1       ──┤
  Cdflgi   67       ──┤
  Cdbu     68       ──┤
  Cdfl     66       ──┤
  Cdkä     71       ──┘
  Cdsp     57       ─┐
  Cdsp     58       ─┤
  Cddu     56       ─┘
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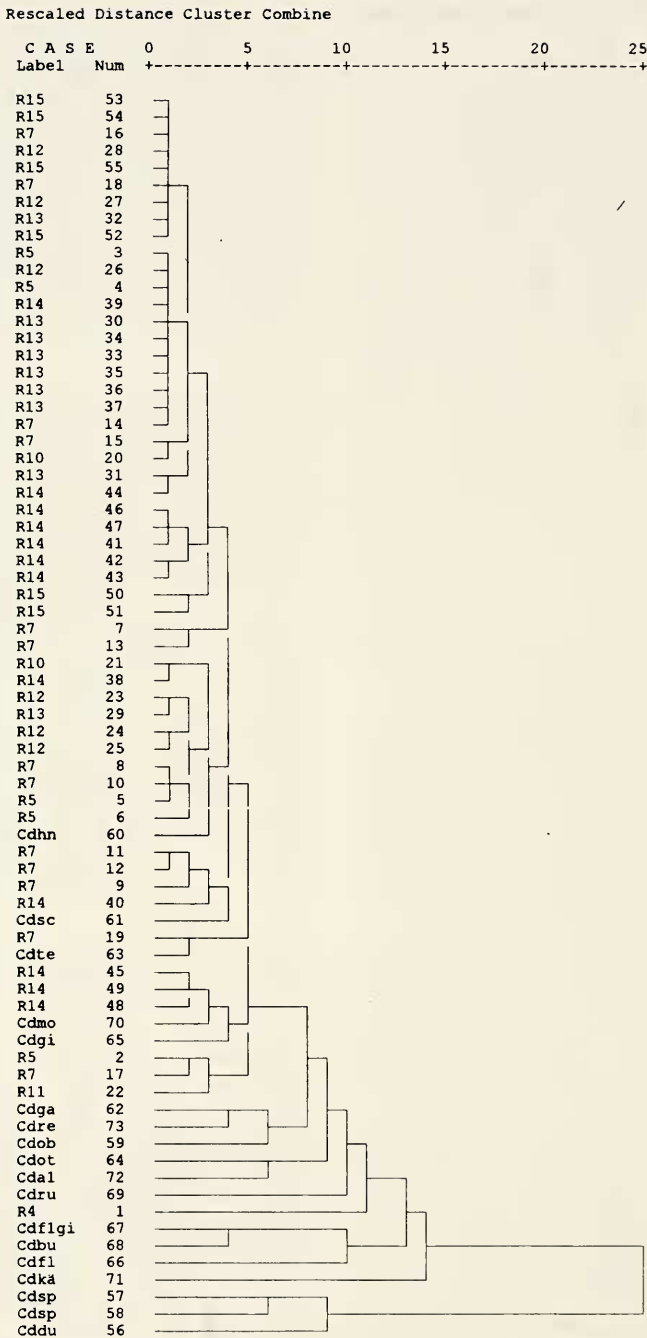
Figure 18. Hierarchical cluster of a spot check of all samples of the Rax area and the SMF specimens. Abbreviations as in Figure 14.
Figura 18. Cluster de todas las muestras del área de Rax y los especímenes SMF. Abreviaturas como en la Figura 14.

Other ecological factors may be of relevance, but we must consider them as arranged in ensembles and affecting upon animals collectively.

Certainly, individual living conditions, as well as hereditary dispositions, result in specific modifications of characters. nevertheless we can reject the hypothesis of EDLINGER AND MILDNER (1982) that the characteristics of *Clausilia dubia runensis* might be a result of helminth parasitism.

A representation of variability of species or populations by character analysis also has to take into consideration the fact that many characters act as correlated variables. In these cases one can speak of character complexes. Arrangements in complexes restrict variability. The question arises, whether there are other factors influencing the variables mentioned above, which are not subjects of the researches presented above. Shells, for example, function as hard skeletons and as mechanical abutments for musculature. Hard skeleton and musculature must be suited to each other. So it is evident, that morphological relations between various measures of the shell are indirectly caused by constructional needs of the animal as a whole and also of the soft body in particular (GUTMANN, 1989; EDLINGER, 1991).

Considering the local patterns of distribution of values and primary components inside the species and its populations, these patterns must be seen as varying locally and gradually. The variation of patterns must be seen as the result of local variation, following from step by step changes of frequencies of characters. When different frequencies are developed under similar ecological conditions, we may assume that these changes are a result of genetic drift.

Certain local accumulation of special characters resp. values of variables may result from genetic drift too. Typical characters of the so called *"Clausilia dubia runensis"*, *C. d. speciosa* (shell form) or *"C. d. otvinensis"* (distances between shell ribs), for example, occur in separate areas with large distances between them. Other characters of the same animals very often don't differ from that of surrounding populations in adjacent areas (EDLINGER AND FISCHER, 1997).

This leads us to the conclusion that frequencies of special characters cannot automatically be taken as a reason for a common origin of separated populations resp. of a heterogeneous origin of contiguous populations. Above all this is true, when other characters are identical with those of contiguous populations.

So it may be that genetic drift or special environmental factors have an influence on single characters. With regard to these characters we may conceive of some populations as homogenous and "pure bred". At the other side there cannot arise populations being homogeneous and "pure bred" in all or most characters and containing such a high number of "typical specimens" homogenous in most or in all characters by simple environmental influences.

In any case, "typical" or "pure bred" specimens were recognized mostly by earlier researchers, and are extremely arbitrary. So, the natural populations of *Clausilia dubia* which were investigated do not match the preconceived expectations of well established races or subspecies occurring in well delimited areas with rare interbreeding occurrences. Therefore, we must question, if a morphologically uniform population of *Clausilia dubia* which can be defined as a subspecies or race, might ever have existed in the eastern Alpine region.

KLEMM (1960) who was of the same opinion, believed that the transitional stages between the races and subspecies might be the consequence of (post glacial) re-immigration of pure bred populations, and their subsequent mixing with other local forms.

Shell characters, and their distribution patterns do not support this hypothesis. Additionally, cluster analysis shows that very variable samples come from regions where the forerunners of present populations must definitely have lived and survived during the Pleistocene. Contrary to KLEMM (1960), we must state that a reconstruction of

events after the Pleistocene gives us no evidence to support this view. Why should areas, glaciated during the Pleistocene be resettled by the descendants of single, pure bred populations after the disappearance of the ice?

A new interpretation of character distribution seems to be more adequate for the case presented, and discussed here. This interpretation requires the (for the case discussed here) use of theorems which are accepted by most anthropologists (CAVALLI-SFORZA, MENOZZI AND PIAZZA, 1994; KLEIN, TAKAHATA AND AYALA, 1994).

According to their theoretical guidelines, the definition of subspecies and race depends on subjective argumentations, and does not mirror objective,

concrete facts. They also accept diversity within given populations. Therefore, distribution and frequency of characters are subject to constant change.

Thus, in any investigated snail population, only the distributions of characters, and the frequency of their occurrence can be reasonably recorded. This entirely altered interpretation also corresponds better with the results of genetic analysis in various species of *Albinaria* (MYLONAS, KRIMBAS, TSIAKAS AND AYOUNTANTI, 1990; SCHILTHUIZEN, 1994). The results of these studies show that there is an overlap of genetic features in some of the traditionally recognized subspecies, and even of species. Similar results may be expected for *Clausilia dubia*.

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